LIFE CYCLE, DISTRIBUTION AND ABUNDANCE OF *CARCINONE-MERTES EPIALTI,* A NEMERTEAN EGG PREDATOR OF THE SHORE CRAB, *HEMIGRAPSUS OREGONENSIS,* IN RELATION TO HOST SIZE, REPRODUCTION AND MOLT CYCLE

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The conceptualization of the host as a microenvironment for the symbiont (Pavlovski, 1934) provided the seed for the growth of the field of parasite ecology. However, the difficulties involved in quantifying the biology of two disparate organisms, host and parasite, have impeded the study of host-symbiont systems from an ecological perspective. As hosts, arthropods lend themselves well to symbiont population studies. Cyclical events through the course of successive molt cycles impose many restrictions on aspects of host growth and reproduction. Thus, many host life history events are discrete and amenable to quantification.

In this study populations of the nemertean egg predator, *Carcinonemertes epialti* Coe, 1902 were monitored in relation to the biology of its host, *Hemigrapsus oregonensis* (Dana, 1851), a common intertidal shore crab along the west coast of North America. Adult specimens of *C. epialti* are only found within or adjacent to egg masses of female crabs. They live in mucoid tubes of their own construction. Since *C. epialti* adults feed on crab eggs, host reproductive conditions are a primary factor in the worm's biology.

The nonfeeding juvenile portion of the nemertean's life cycle is spent ensheathed on the exoskeleton of host crabs of either sex. Newly molted crabs lack nemerteans. The nemertean population of the previous instar is shed at ecdysis. Nemertean transmission through a host molt cycle should result in increasing nemertean density on the host with advancing stages in the molt cycle. Furthermore, crabs with longer intermolt cycles, such as large crabs, should tend to have more nemerteans. Thus, *C. epialti* is regarded as a population of animals disseminating through a habitat which consists of systematically renewed substrates, crab exoskeletons. Access to the host cuticle can be partially estimated by a size and sex-specific determination of the host's molt stage. Several studies have compared the biology of epizoic organisms with the general pattern of the host molt cycle. Barnacles have been used to estimate the molting frequency of lobster (*Nephrops*) hosts (Barnes and Bagenal, 1951). The barnacle *Trilasmis* reproduces more frequently than the average spiny lobster host intermolt duration, assuring continual replenishment of epizoic populations (Bowers, 1968). Apostome ciliates excyst and initiate feeding at host ecdysis (Trager, 1957; Bradbury and Trager, 1967). Peritrichous ciliates swarm at ecdysis of the gammarid amphipod host (Fenchel, 1965). The bryozoan, *Triticella koreni,* metamorphoses only on the cuticle of a recent postmolt *Calocaris* (Thalassinidea) (Ström, 1969), and the colony produces embryos just prior to the annual molt of the host (Ström, 1969;

Eggleston, 1971). Total abundance of epizoic hydroids, bryozoans and barnacles is greater on crabs (*Bathynectes*) in late postmolt (C_{1-3}) plus intermolt (C_4) molt stages than on early postmolt (A_1–B_2) stages (Lewis, 1976). The present study, employs the molt-staging scheme of Drach (1939; Drach and Tchernigovtzeff, 1967) to examine epibiont-host synchrony in detail.

The intricate exoskeletal morphology of an arthropod offers unique opportunities for studies of habitat preference and utilization. Here is a habitat which is varied, yet standardized. A given pit or groove varies in a manner that lends itself to a reasonably simple quantitative description. Studies of habitat exploitation and selection for epizoic forms on crustacean hosts have rarely (Walker, 1974) reached the level of sophistication demonstrated in studies of water mites on aquatic insects (Efford, 1965; Mitchell, 1967, 1968; Lanciani, 1970, 1971; Davids, 1973).

Although egg predators of crustaceans are common (Kuris, 1971), few population studies have been conducted. Humes (1942) and Hopkins (1947, 1970) describe the life cycle of *Carcinonemertes carcinophila* on the blue crab, *Callinectes sapidus,* in detail. Wickham (1977) describes a new distinctive species of *Carcinonemertes* from *Cancer magister* and indicates (Wickham and Fisher, 1978) that it is responsible for considerable brood mortality in this commercially important species.

Other than the original description from the kelp crab *Pugettia producta* (Coe, 1902) and a host (*Euphylax dovei*) and range extension to Payta, Peru (Humes, 1942), *C. epialti* is unstudied. *Carcinonemertes epialti* occurs on *H. oregonensis* at 13 localities from Bahia San Quintin, Baja California, Mexico, to Page's Lagoon, British Columbia, Canada (Kuris, 1971). The geographic distribution on the Pacific Coast of North America appears to be continuous between these two localities.

Materials and Methods

Field studies were conducted at Campbell Cove, Bodega Harbor, Sonoma County, California, during 1969–1971. Additional collections were made during the summers of 1973–1975. Material for some studies was sometimes collected elsewhere in Bodega Harbor. *Hemigrapsus oregonensis* was collected monthly from randomly placed removable substrate traps (sampling program detailed in Kuris, 1971), and the nemertean populations were censused. Supplementary host samples were collected by hand and at random without regard to size, sex or reproductive condition.

During April-May, 1969, and June-July, 1970, a survey of 26 populations of *H. oregonensis* was conducted along a transect from Bahia San Quintin, Baja California, Mexico, to Ucluelet, Vancouver Island, British Columbia, Canada. These collections, of 75–150 adult crabs each, greatly extended the geographic range of *C. epialti*. Station records are given in Kuris (1971).

From all crabs the following was recorded: carapace width to 0.1 mm, taken with a vernier caliper at the notch immediately anterior to the third lateral spine; sex; and molt cycle stage according to the scheme of Drach (1939) and Drach and Tchernigovtzeff (1967). Criteria and techniques used for molt stage assignment are given in Kuris (1971). For ovigerous female crabs the embryogenic process

was divided into 20 egg development stages based on cell number, amount of yolk remaining and appearance of various embryonic structures (Kuris, 1971).

All hosts were sampled by inspection of the external surface of the exoskeleton. Special attention was paid to the branchial chamber, the sternal-abdominal furrow and the pereiopod axillae. As the crustacean exoskeleton is a very complex but highly standardized structure, site specificity of *C. epialti* was detailed by subdividing the host's surface into 150 potential sites on male crabs and 160 sites on female crabs. Adult nemerteans and their eggs were only observed on ovigerous female crabs. Adult nemerteans were removed, then sized and sexed using a compound microscope.

Transmission of juvenile nemerteans was tested experimentally. Lightly infested hosts were examined daily, and all visible nemerteans were removed. These hosts were regarded as clean when no nemerteans were recovered on three successive days. One group each of three individual cleaned males, females with ripe ovaries (pre-ovigerous) or ovigerous females with broods in an early stage of embryogenesis was exposed to a single heavily infested (10 + nemerteans) male crab. Thus, four crabs, one infested, and three cleaned, were confined together in perforated 14 mm $\times$ 10 mm $\times$ 4 mm hard plastic boxes maintained in running sea water. Controls for each of these three combinations were run simultaneously by using a cleaned male in place of the infested male. A gravel substrate and a few small rocks for cover were provided in each transmission box. Crabs were fed *Ulva* every other day. All crabs were marked individually by a tattoo method (Kuris, 1971). The transmission experiments were conducted in July and August, during the period of peak nemertean abundance.

The number of nemerteans on the infested and clean crabs were recorded on the experimental days 7 and 14. The experiments were terminated on experimental day 14, at which time the crabs were dissected and exhaustively searched for the presence of nemerteans. The entire transmission experiment was replicated once.

Results

Host specificity

In the Campbell Cove, Bodega Harbor, study area, *Carcinonemertes epialti* is regularly found on *Hemigrapsus oregonensis*, with *H. nudus* serving less frequently as a host. In the lower reaches of the intertidal, *Carcinonemertes* species also occur regularly on *Cancer antennarius*, *C. anthonyi*, and *C. productus* juveniles and adults.

Important negative records based on hundreds of observations include *Pachygrapsus crassipes*, and the anomurous crab, *Petrolisthes cinctipes*. No nemerteans were ever found on the surface of 45 juvenile *Pugettia producta* from the shallow subtidal regions adjacent to the study area. A search of about 50 female ovigerous *P. producta* from elsewhere along the Sonoma coast produced a single positive record (recovered by R. I. Smith and examined by the author). However, *P. producta* from the Santa Barbara Channel is more frequently infested by *C. epialti*.

Life cycle

Extrusion of an egg mass by a nonovigerous female crab signals the start of the reproductive phase of the nemertean life cycle. Juvenile nemerteans ensheathed on
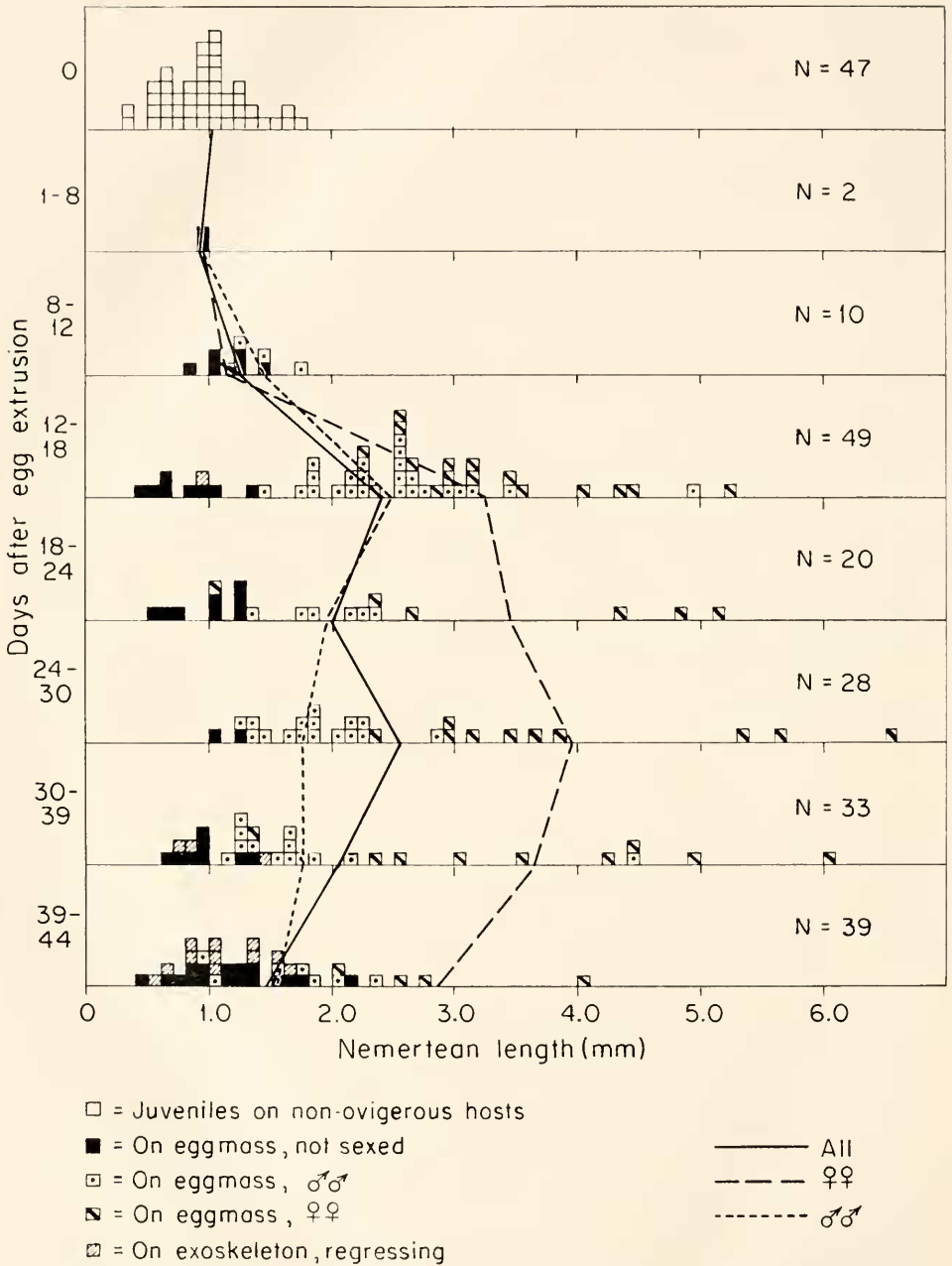
FIGURE 1. Size-frequency histogram, representing the population structure of *Carcinonemertes epialti* during the period of host egg development. Average sizes of sexable males (short dash line), females (long dash line) and the entire sample (solid line) are superimposed on histogram.

regions of the exoskeleton remote from the host egg mass exsheath and migrate to the pleopods or sternal surface of the thorax and abdomen. Here each individual constructs and inhabits a mucous tube. Occasionally, both sexes may be found within the larger female tube. A gravid *C. epialti* female deposits her eggs in the posterior portion of her mucous tube. No nemertean egg tubes are found on crabs with embryogenesis less advanced than initiation of thoracic limb development which is reached 18 days after host oviposition (Kuris, 1971). Embryogenesis advances until thoracic limb buds are large before hatching nemertean eggs are observed. At 10–12° C thoracic limb bud development takes 8 days (Kuris, 1971). This interval estimates the duration of nemertean embryogenesis. Nemertean oviposition may proceed for the next 25 days, until host eclosion. Nemertean egg hatching may continue five days subsequent to the hatching of the crab eggs.

Growth of the nemerteans, on the host's egg mass from the time of host egg deposition, is rapid (Fig. 1). From the average juvenile length of 1.0 mm, female worms grow to an average adult size of 3.9 mm 24–30 days after the host becomes ovigerous. Males grow more slowly, reaching an average of 2.5 mm 18–24 days after egg extrusion. Thirty days from the time of egg deposition, some of the nemerteans begin to regress, even to leave the egg mass and retire to the other sites on the crab. By the time the zoeae hatch, the average sexable adult females are 2.8 mm; the males, 1.6 mm. Both of these values probably over-estimate the size of adult worms, as regression below 1.5 mm makes sexing difficult. The average size of all worms on egg-bearing females reaches a maximum of 2.5 mm by 30 days after egg deposition, and then declines to 1.4 mm by the time the host's brood hatches, 44 days after having become ovigerous.

The nemertean's modified (Hyman, 1951) pilidium larva appears to be planktonic for an unknown period of time. Ultimately, this dispersal stage must settle on a crab host and transform to a juvenile.

Crab hosts of either sex, mature or not, may become infested with juvenile *C. epialti*. However, only when ovigerous or pre-ovigerous crabs are infested may the life cycle be completed.

Some of these larval and juvenile nemerteans reach pre-ovigerous female hosts. The sites occupied by juveniles on such crabs are similar to those occupied by juveniles on nonovigerous hosts. However, a day or two after a pre-ovigerous host undergoes oviposition, virtually all the juvenile nemerteans ensheath and migrate to the vicinity of the host's egg mass. Here the nemerteans begin a period of rapid growth, sexual differentiation and maturation. Copulation presumably occurs when the male nemertean enters the female's mucous sheath.

As the host's eggs near the date of hatching, the nemerteans cease to grow (Fig. 1). Some worms leave the egg mass, frequently migrating to sites within the branchial chamber of the host. The anterodorsal surface of the host's branchial chamber is frequently occupied by these worms. Here they ensheath, decrease in size, and become reproductively inactive. Soon they are indistinguishable from juvenile nemerteans. Some of the post-reproductive worms may die rather than regress. Large, seemingly moribund individuals are seen shortly after eclosion of the host brood. These worms may merely be undergoing negative growth, however. Whether secondarily reduced, post-reproductive worms are capable of another reproductive period is unknown.

TABLE I

Experimental transfer of juvenile C. epialti *from heavily infested male crabs (donors)
to uninfested male and female (ovigerous and nonovigerous) hosts.*

Experimental combination	Number of hosts	Number of worms removed prior to start	Number of worms observed on day			Number of worms after dissection	Number of worms unaccounted for	Mean worm density on recipients day 14
			0	7	14			
Donors	2	—	54	31	14	22	18	—
Recipient males	6	3	0	7*	11	14	—	2.3
Donor control	1	0	0	0	0	0	0	—
Recipient male controls	3	6	0	1	1	1	—	0.3
Donors	2	—	100	75	57	69	19	—
Recipient non-ovigerous females	6	4	0	1	6	12	—	2.0
Donor control	1	0	0	0	0	0	0	0
Recipient non-ovigerous female controls	3	5	0	3	3	3	—	1.0
Donors	2	0	115	105	68	75	12	—
Recipient ovigerous females	6	2	0	5	12**	14	—	4.0
Donors control	1	0	0	0	0	0	0	—
Recipient ovigerous female controls	3	3	0	2	2*	2	—	1.0

* One recipient died prior to observation date, data for day 14 based on 2 donors and 5 recipients.

** One donor died prior to observation date, data for day 14 based on 1 donor and 3 recipient crabs.

Based upon microscopic examination of the gut, host eggs appear to be the only source of nutrition for the adult worms. Juvenile worms appear to have empty digestive tracts. Thus, it is not surprising to find that growth of juvenile worms on male hosts, juvenile females, or nonovigerous adult females is quite restricted. The size range of juvenile nemerteans from these sources is only 0.4 to 1.6 mm. These juveniles are considered to be essentially phoretic on the host crab. Since the newly-hatched larvae are 0.2 mm long, little food seems to be required for transformation to the juvenile form, and subsequent maintenance on the host exoskeleton. The source of energy for this maintenance remains unknown.

Transmission

It is likely that there are two modes of transmission for *C. epialti*. The free-swimming larval stage facilitates interhost transmission. Incidents of direct contact between hosts, followed by transferral of juvenile worms, may also enable transmission to occur. Direct transmission was tested experimentally.

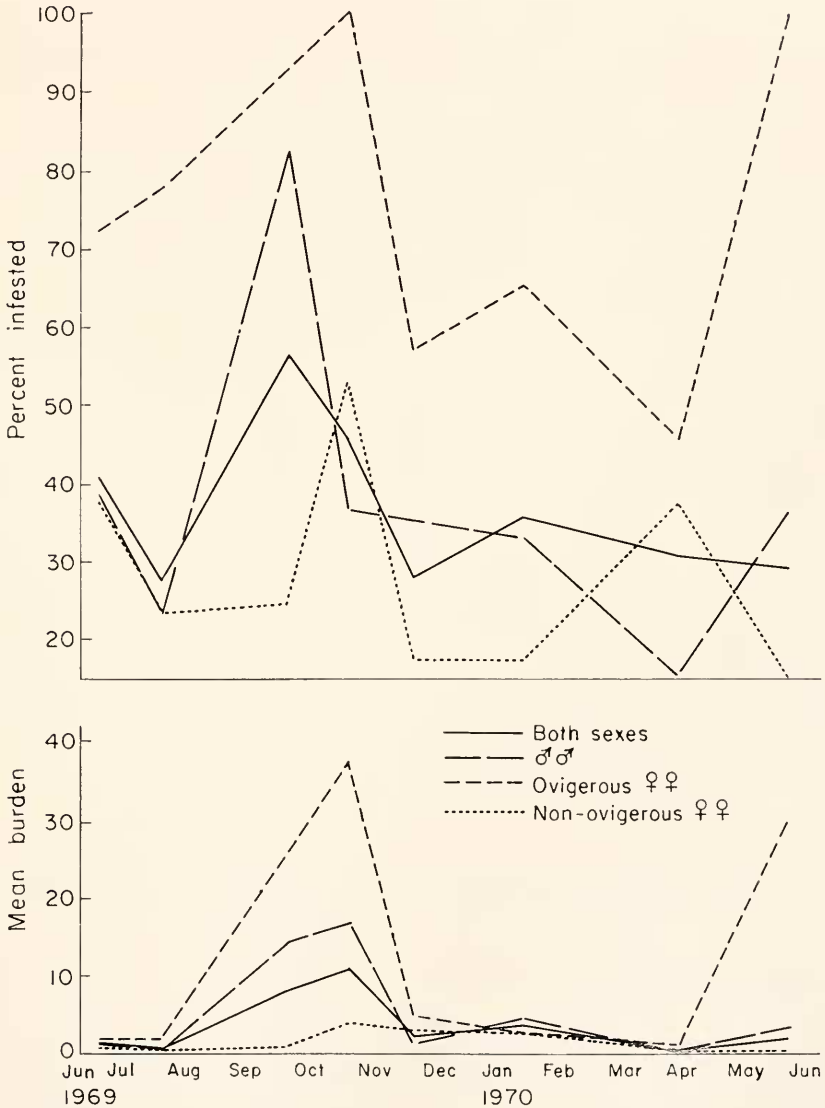*Carcinonemertes epialti* on *Hemigrapsus oregonensis*
Seasonal Changes

FIGURE 2. Seasonal pattern of the percentage of infestation (top) and mean burden (mean density per host) (bottom) for all hosts, ovigerous females, nonovigerous females and males over 8 mm, at Bodega Harbor.

Table I shows that significant transfer (G-test, day 14, $P < 0.05$) of juvenile nemerteans may occur between hosts and suggests that ovigerous hosts may elicit more transferrals than nonovigerous hosts. The occasional nemerteans seen on the externally cleaned and unexposed control crabs are probably derived from sites hidden within the host's branchial chambers, inaccessible to the removal-trapping method of cleaning crabs.

Infestation frequency and nemertean density

Seasonal variation. For 741 crabs greater than 8.0 mm wide, the overall infestation rate for 1969–70 at Bodega Harbor was 36.3%. Burden, the mean density per host (including uninfested hosts), was 3.96.

Through the sample year, the infestation level of *C. epialti* on *H. oregonensis* varied from 28% to 57%. Figure 2 shows that the overall infestation rate actually remained steady at 30–40%, except for the September and October samples, which reached 57% and 46%, respectively. This rise occurs when the host population is reproductively inactive while undergoing the final ecdysis prior to the onset of the winter anecdysial period (Kuris, 1971). The maturation of large juvenile and prepuberty female hosts also occurs at this time; so virtually all the crabs over 8.0 mm are adults in the coming winter reproductive season. The nemertean density per host reflects this pattern, rising to an October peak density of 11 worms per host. Excepting the autumn samples, worm burden ranges from 0.5 to 4.0 worms per host. Surprisingly, the peak period of crab reproduction, November to February (Kuris, 1971), is the interval of lowest nemertean density (Fig. 2).

Host reproduction. The importance of host reproduction to population dynamics of *C. epialti* is seen in Figures 2 and 4. In all seasons the frequency of ovigerous female crabs harboring nemerteans is higher than that of nonovigerous females or males. With the exception of the January sample, this is also true of the average nemertean density per host crab over 8 mm.

As host eggs proceed through embryogenesis, an increase in nemertean prevalence and density might be expected on ovigerous crabs (Table II). The percentage of infestation increases slightly, from 62.9% of broods in embryogenic stages to 73.7% of broods in late stages, with slight fluctuations at intermediate stages. Burden (b) remains essentially the same (4.2–4.4) from early through late middle egg development stages. However, b̄ then rises sharply, to 8.11 in late stage broods.

During host embryogenesis the worms anchor their mucous sheaths and feed while protruding from the open end. The nemerteans are able to feed on the eggs if their sheath is entwined among the host egg mass or is attached to the abdominal appendages or the sternal surfaces of the abdomen and the thorax. On nonovigerous adult female crabs only 73.3% of the nemerteans are found in the vicinity of the egg mass. However, almost immediately after deposition of the host's brood, 95.9% are near the egg mass. This distribution pattern remains almost constant for the first 26 days of host embryogenesis. Towards the end of the brooding period, a gradual withdrawal to other sites is evident (Table II). Only 64.7% of the nemerteans remain at sternal locations on post-ovigerous female crabs.

Host molt cycle. Figure 3 shows the changes in nemertean burden on similar-
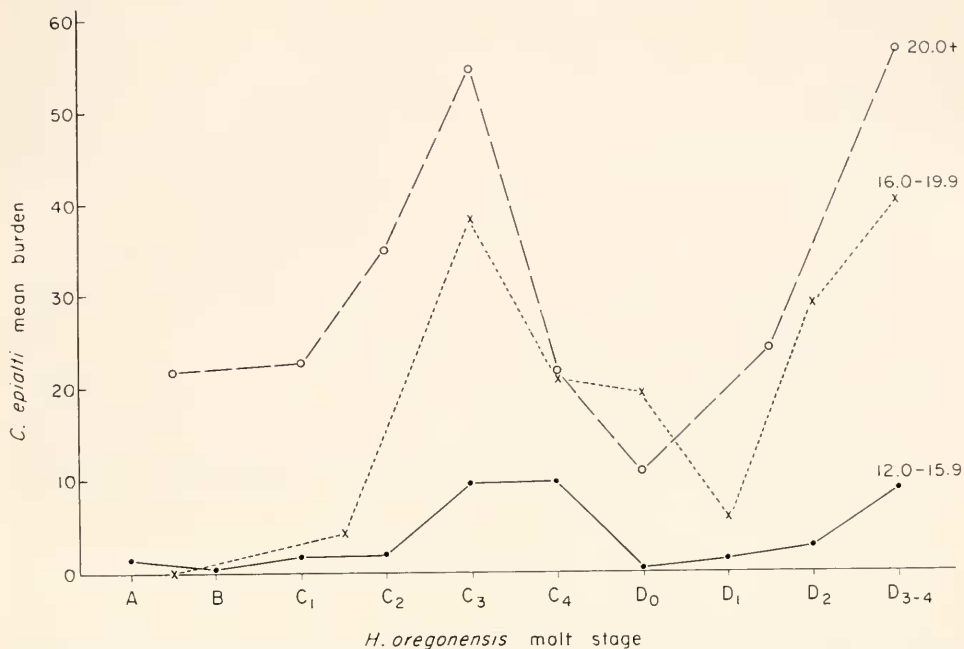
FIGURE 3. Average burden (mean density per host) of *Carcinonemertes epialti* on different sized male *Hemigrapsus oregonensis* in different stages of the molt cycle.
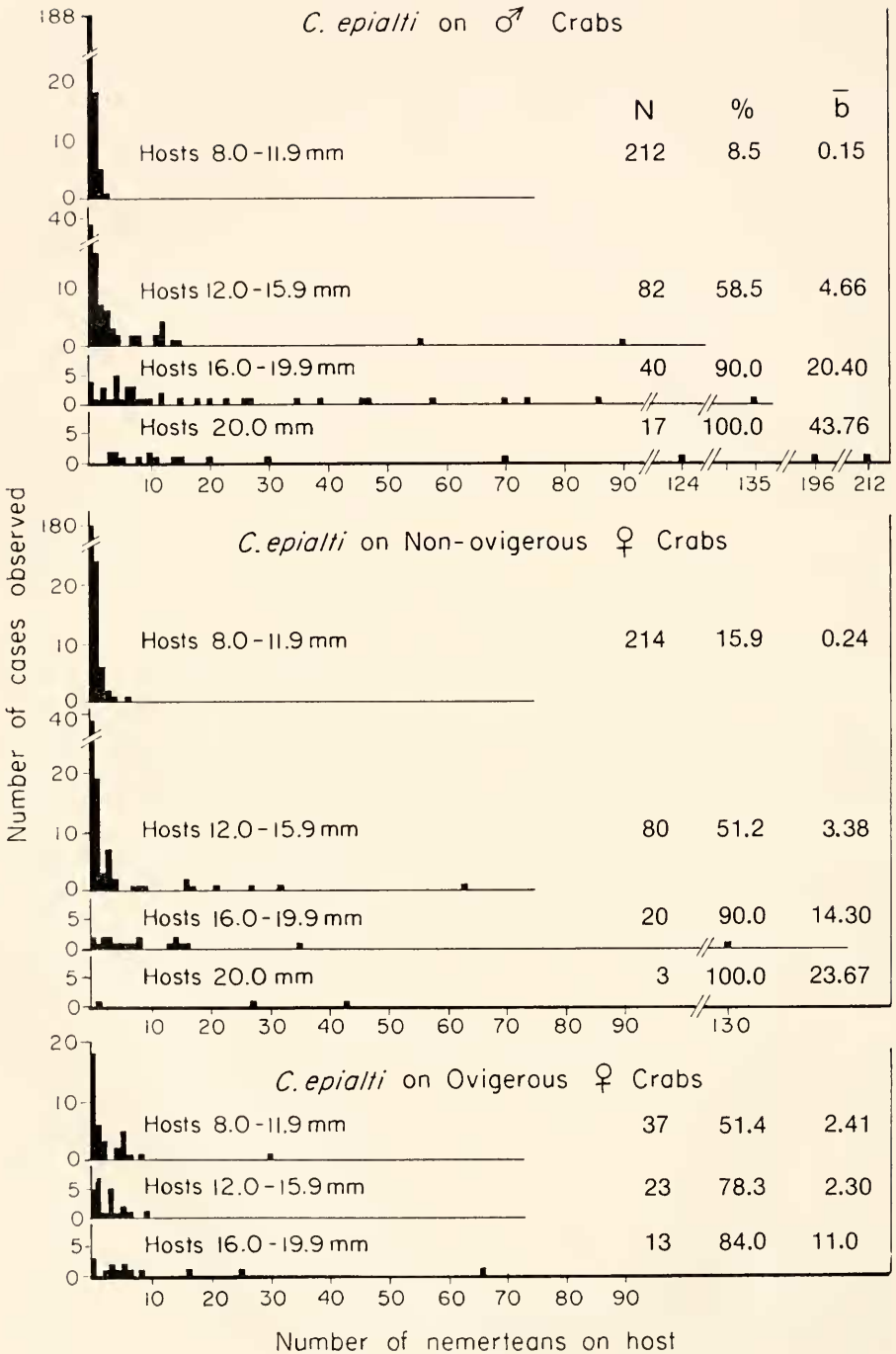
sized male hosts, with successive molt stages. The average burden is seen to rise sharply from Drach molt stages A to C_3 or C_4. However, from C_4 or D_0 to D_1 there is a sharp drop in average density per host; this is followed by an equally sharp rise in late premolt, D_2-D_4.

Host size. Figure 4 shows that both nemertean incidence of infestation, and the average burden, increase dramatically with increasing host size. Ovigerous females, while showing some size effects (Fig. 4 bottom), do not show as sharp an increase in average density with increasing size as do males and nonovigerous females. The incidence of infestation among different size classes is significant

TABLE II

Percentage infestation (%i), average burden ($\bar{b}$), and site preferences of C. epialti *on ovigerous crabs through the course of embryogenesis. Post-ovigerous crabs are also included.*

Egg development stages (grouped)	n	%i	$\bar{b}$	Percentage of nemerteans on egg mass and on thoracic and abdominal sterna	Percentage of nemerteans at other sites
Early (1 to 12 days)	35	62.9	4.2	95.9	4.1
Early middle (13 to 26 days)	58	74.1	4.4	95.7	4.3
Late middle (27 to 37 days)	38	76.3	4.3	88.1	11.9
Late (38 to 43 days)	19	73.7	8.1	73.2	26.8
Post-ovigerous (duration uncertain)	11	72.7	17.0	64.7	35.3

C. epialti on ♂ Crabs

	N	%	$\bar{b}$
Hosts 8.0 - 11.9 mm	212	8.5	0.15
Hosts 12.0 - 15.9 mm	82	58.5	4.66
Hosts 16.0 - 19.9 mm	40	90.0	20.40
Hosts 20.0 mm	17	100.0	43.76

C. epialti on Non-ovigerous ♀ Crabs

Hosts 8.0 - 11.9 mm	214	15.9	0.24
Hosts 12.0 - 15.9 mm	80	51.2	3.38
Hosts 16.0 - 19.9 mm	20	90.0	14.30
Hosts 20.0 mm	3	100.0	23.67

C. epialti on Ovigerous ♀ Crabs

Hosts 8.0 - 11.9 mm	37	51.4	2.41
Hosts 12.0 - 15.9 mm	23	78.3	2.30
Hosts 16.0 - 19.9 mm	13	84.0	11.0

Number of cases observed

Number of nemerteans on host

(G-test, $P < 0.001$) for males and nonovigerous females and for ovigerous females ($P < 0.05$).

Within each size class there is no significant difference between the three reproductive classes except for the 8.0–11.9 mm size class ($P < 0.005$). Relatively high levels of infestation among small (8.0–11.9 mm) ovigerous females account for both the generally high infestation rate of ovigerous females compared with males and nonovigerous females, and the significant difference in incidence seen among the reproductive categories for the smallest size class.

Two changes in the pattern of nemertean abundance occur as host size increases. The frequency of uninfected crabs drops sharply (91.5% to 0.0%) with increasing size. Also, the frequency of heavy infestations, $\bar{b} > 9$, increases strongly, from 0.2% to 65.0%. These trends with increasing size result in contagious distribution patterns; the variance to mean ratio (coefficient of dispersion) greatly exceeds one in all groups over 12 mm. Even in the 8–12 mm size classes, the coefficient of dispersion is over one, indicating that these samples are also clumped. Tests for goodness of fit (χ^2, Sokal and Rohlf, 1969) result in highly significant differences from the expected Poisson distribution in all 4 mm size classes for male, ovigerous female and nonovigerous female hosts.

Site specificity

The distribution of nemerteans is analyzed here for male crabs only. Nemerteans on nonovigerous crabs have a similar pattern of occurrence, differing only in the details of female *versus* male sternal anatomy.

On male crabs fifty of the sixty investigated sites harbored *C. epialti* with some regularity. The most frequented sites include the anterior face of the arthrodial membrane at the base of the coxa of the fourth walking leg, the posterior face of the equivalent membrane of the cheliped, and the ventral angles of the axillae between the second and third, and third and fourth walking legs. Other points at the bases of the limbs were only slightly less commonly utilized as sites. In general, locations in the second axilla, between the first and second walking legs, were the least commonly inhabited sites on the limb bases. In the sternal-abdominal furrow, the anterior sternal sutures of the thorax, the bases of the copulatory pleopods, and the anterior segments of the abdomen were often frequented. In the gill chamber, the fourth and fifth thoracic epimera and the vicinity of the pericardial sacs were commonly utilized sites.

A single case of internal infection of *H. oregonensis* by *C. epialti* was observed. Three juvenile nemerteans were found in the posterior portion of the host's intestine. Occasionally, juvenile nemerteans are wedged deeply into the apodemes originating from the branchial region of the thorax. Superficially, these resemble internal infections. Exsheathed juveniles are occasionally found actively wandering about the host surface.

FIGURE 4. Size frequency histogram for *Carcinonemertes epialti* on different size classes of 351 male, 317 nonovigerous and 73 ovigerous female *Hemigrapsus oregonensis*. N. is the sample size; %i is the percentage infested; and $\bar{b}$, mean burden, is mean density per crab (including uninfected crabs). For all male crabs %i $= 36.0\%$, $\bar{b} = 5.70$; for all nonovigerous females %i $= 30.3\%$, $\bar{b} = 2.14$; for all ovigerous females %i $= 65.8\%$, $\bar{b} = 3.90$.

<div align="center">TABLE III</div>

Site utilization by C. epialti on male H. oregonensis at different host sizes. All densities of worm infestation are included. See text for descriptions of site regions I–IV. The percentage of nemerteans in a region is in parentheses; b is the number of nemerteans; i is the number of hosts infested. $G_H = 93.268$, P < 0.005; an a posteriori STP shows that the two smallest and three largest size classes constitute homogeneous sets.

Host size group (in mm)	b at sites				Σb	i	$\frac{\Sigma b}{i}$
	I	II	III	IV			
8–11.9	4 (5.6)	3 (4.2)	64 (88.9)	1 (1.3)	72	44	1.64
12–15.9	28 (4.1)	80 (11.6)	566 (82.1)	15 (2.2)	689	83	8.30
16–19.9	136 (7.5)	418 (22.9)	1243 (68.1)	27 (1.5)	1824	68	26.82
20+	182 (7.5)	578 (24.0)	1614 (66.9)	39 (1.6)	2413	76	31.75
	350	1079	3487	82	4998	271	18.44

To examine the relationship between host size and site specificity, potential sites were grouped into four regions. (I) branchial chamber-pericardial; (II) sternal-abdominal furrow; (III) interlimb axillae; (IV) miscellaneous (mouthparts, exposed body surface). Table III indicates that only region II shows a progressive increase in the percentage of site utilization of *C. epialti* with increasing host size. The heterogeneity G-test statistic (G_H; Sokal and Rohlf, 1969) is highly significant; size-specific site utilization is not homogeneous. As there is significant heterogeneity among size classes, an *a posteriori* test by a simultaneous test procedure (STP) of the different sizes for goodness of fit (Sokal and Rohlf, 1969) is used to locate the source of the heterogeneity. The results of the STP using the G-statistic indicate that a highly significant difference in the frequency of the nemertean at certain sites occurs between small (≤ 15.9 mm) and large (≥ 16.0 mm) crabs. Apparently, some of the sites in the sternal-abdominal furrow are not available to the nemerteans on small crabs. Presumably due to spatial considerations, these sites become available on crabs over 16.0 mm.

Changes in site utilization in relation to nemertean density were analyzed in a similar fashion to the site-host size relationship. Infested crabs were apportioned

<div align="center">TABLE IV</div>

Shift in site preference with changes in nemertean density on H. oregonensis. All sizes of infested hosts included. Site regions I–IV are described in text. The percentage of nemerteans in a region is in parenthesis; b is the total number of nemerteans; i is the number of hosts infested. $G_H = 110.186$, P < 0.005; an a posteriori STP disclosed these homogeneous sets: a) 1–10, 11–19, 20–49, b) 20–49, 100+, c) 1–10, 11–19, 50–99.

Range of worm burdens	I	II	III	IV	Σb	i	$\frac{\Sigma b}{i}$	Mean host size
1–10	47 (8.2)	90 (15.6)	435 (75.5)	5 (0.0)	577	156	3.70	15.6
11–19	19 (5.0)	67 (17.7)	286 (75.7)	6 (1.6)	378	29	13.03	18.0
20–49	88 (8.5)	217 (20.9)	720 (69.2)	15 (1.4)	1040	31	33.55	19.8
50–99	57 (5.0)	180 (15.8)	876 (77.0)	24 (2.1)	1137	15	75.80	18.8
100+	139 (7.5)	525 (28.2)	1163 (62.6)	32 (1.7)	1859	12	154.92	20.0

among five nemertean density classes (Table IV) without regard to host size; G_H is highly significant. An *a posteriori* STP was performed to locate the source of the heterogeneity. The STP shows that crabs having 20–40 and 100+ nemerteans (Table IV, homogeneous set b) have significantly more nemerteans on region II and fewer on region III than occur at other worm densities (homogeneous set c). Homogeneous set a shows that there is some overlap between sets b and c at these sample sizes.

DISCUSSION

The common occurrence of *Carcinonemertes epialti* on *Hemigrapsus oregonensis* contrasts with its occasional presence on *H. nudus*, its scarcity on *Pugettia producta*, and its absence on *Pachygrapsus crassipes*. The infrequent infestation of *Pugettia producta* (= *Epialtus productus*) by *C. epialti* is of interest, as this is the type host (Coe, 1902). At least along the Sonoma coast, the specific name *epialti* is an unfortunate choice. All the ovigerous specimens of *P. producta* from this region are infested with several hundred turbellarian egg predators of an undescribed species [*Monocelis?* (Sakaji, personal communication)]. The inadequately documented record of *C. epialti* on *P. producta* (Boolootian, Giese, Farmanfarmaian and Tucker, 1959) is probably a misidentification of the undescribed turbellarian. The size (1–2 mm), and the activity, "gliding continually" (p. 219), both fit the turbellarian, and decidedly not *C. epialti*.

The small worms, found on *Cancer magister* by MacKay (1942) and probably misidentified as leeches (Sindermann and Rosenfield, 1967), are most likely the *Carcinonemertes* species to be described by Wickham (1977). Specific identification of the *Carcinonemertes* found on other *Cancer* species awaits further study (Wickham, personal communication).

Humes (1942) observed that 20 of the 26 host records for *Carcinonemertes* spp. available to him were for portunid crabs (including the Peruvian portunid *Euphylax dovei* as a host for *C. epialti*). He considered the littoral Portunidae to be the principal hosts for these worms due to their habits, abundance, and habitat preferences. The host specificity records for *Carcinonemertes* on the Pacific coast of North America, suggest that neither portunids, nor the behavioral and habitat characteristics typically associated with the swimming crabs, are necessarily associated with nemertean infestations.

The Carcinonemertidae are considered to exhibit little host specificity (Humes, 1942). However, the negative records on *Pachygrapsus crassipes*, despite the habitat overlap of these crabs with heavily infected host species, suggests that host specificity does play a part in governing the distribution of *C. epialti*.

A comparison of the life cycle of *C. epialti* with *C. carcinophila* (Humes, 1942; Hopkins, 1947) shows some important differences. The juvenile stage of *C. carcinophila* is found almost exclusively on the gills of the nonovigerous host. This site may indicate a decreased opportunity for interhost transfer of juvenile worms during casual contact. However, frequent transfer during the mating act seems feasible since copulation, followed by a post-mating embrace, is a lengthy process in portunid crabs (Hartnoll, 1969), principal hosts of *C. carcinophila*.

The fate of the post-reproductive adult nemertean is another potentially distinctive species difference. In *C. carcinophila* the adult worms retire to the gill chamber

of the host upon hatching of the crab's brood (Humes, 1942; Hopkins, 1947, 1970). Here they can be distinguished from pre-reproductive juveniles by their bright red color. The principal western Atlantic host, *Callinectes sapidus*, ceases to molt upon reaching adulthood (Van Engle, 1958), and thus the nemerteans are never shed after the host's eggs hatch. Hopkins (1970) feels that they also return to the host's egg-mass during the next ovigerous period. Since Hopkins (1947) describes the post-reproductive worms in the gill chambers as "large," there is an indication that the post-reproductive worms do not regress to the size of the juvenile worms upon their return to the gills.

Both juvenile transfer and larval settlement are regarded as important factors of a transmission model accounting for the distribution of nemerteans on host crabs. It is proposed that larval settlement of a short-lived larval phase accounts for the occasional occurrence of heavily infested crabs. Since *Hemigrapsus oregonensis* spends long periods of time aggregated under covering rocks (Kuris, unpublished mark recapture study), they may occasionally encounter a dense larval swarm in the small volumes of water with restricted circulation in this confined habitat. The considerably greater surface area of larger crabs available for settlement, as well as the occurrence of additional suitable sites for juvenile worms on such crabs, may result in most of the heaviest infestations being found on these crabs. As most large crabs are males, this would also account for the more frequent occurrence of large numbers of juvenile nemerteans on males.

Transferral of juvenile nemerteans from infested to uninfested hosts through accidental and mating contact may be the means by which most crabs with low nemertean burdens (1 to 10) become infested, as such contacts are of short duration (Knudsen, 1964; Kuris, 1971). Also, most juvenile nemerteans are usually surrounded by a thin mucous sheath; for host transfer to occur they must escape the sheath. Thus, only a small percentage of the population of nemerteans are available for contact transmission at a given instant.

The laboratory transmission experiments indicate that juvenile transferral occurs between donor males and recipient males, nonovigerous females, and ovigerous females. Perhaps such transfers also occur with donor nonovigerous females. However, it seems likely that transfers from ovigerous female crabs are much less likely to occur. Thus, ovigerous females come to have a much higher mean percentage of infestation, 65.8%, than do either males, 35.6%, or nonovigerous females, 30.3%. That this difference is a result of transfer interactions rather than more favorable conditions for larval settlement is shown by the higher frequency of low nemertean burdens on the ovigerous females than on the other classes of hosts (Fig. 4). Were larval settlement to be enhanced on ovigerous females, then the frequency of the heavy nemertean burdens, presumed to be due to larval transmission, would be greater on these females.

Most large crabs, especially those over 16.0 mm, are infested without regard to reproductive state. Thus, only small crabs show the effect of the accumulation of transferred juvenile nemerteans as an increase in the percentage infestation (Fig. 4). If larval nemerteans do not settle preferentially, then the nemertean burden of egg-bearing crabs is increased over nonovigerous crabs only by the number of nemerteans gained by juvenile transfer. In accordance with the transmission model, an increase in the number of nemerteans per ovigerous host over the period

of host embryogenesis is seen (weakly) in Table II, since ovigerous crabs gain but presumably do not lose nemerteans through contact transferral.

The increase in nemertean burden during postmolt stages is also in accord with the nemertean transmission model. However, the intermolt decline and premolt rise in worm abundance for all host size classes indicates that factors other than simple accretion of nemerteans through time are operating. Perhaps male and nonovigerous females lose nemerteans through contact transfer to ovigerous crabs. Crabs avoid contact during postmolt, and copulation is perhaps limited to C_4–D_1 in male crabs (Kuris, 1971). Also, selective transmission to postmolt crabs might give the nemerteans a better chance to locate a pre-reproductive female, or a pre-copulatory male. However, preferential settlement on these stages would not ac-count for the equally dramatic rise in the abundance of nemerteans in D_2–D_4.

The strongly host-size dependent distribution of *C. epialti* does not appear to be due to a nemertean build-up over time on large crabs with long intermolt intervals. Nemertean populations fluctuate over the intermolt period when crab size (and molt cycle duration) is held constant. More likely, crab size directly influences nemertean burdens. Large crabs have relatively more sites to offer nemerteans, and can accommodate larger nemertean populations; also preferred nemertean sites are more spacious on large crabs and can support more worms per site.

If the size of the host influences the availability for nemertean habitation of certain sites on the host's exoskeleton, then the percentage of nemerteans on rela-tively unavailable site should rise as host size increases. Such is the case (Table III). However, nemertean density also influences site occupancy (Table IV). Crowding at high density may result in some individuals occupying suboptimal sites. However, those density classes (20–40, 100+) having the greatest propor-tion of worms at the presumably less preferred sites of region II also have larger mean host sizes (Table IV).

Examination of the interaction between the effects of intermolt interval, site availability and site preference suggests that all three effect the distribution of *C. epialti*. However, the increase in site availability with increasing host size seems to be the most important factor determining site occupancy.

SUMMARY

1. The geographic range of *Carcinonemertes epialti* has been greatly extended. The worms are found from Bahia San Quintín, Baja California, Mexico, to Page's Lagoon, Vancouver Island, British Columbia, Canada.

2. New host records for *C. epialti* include *H. oregonensis,* and *H. nudus.* It is rare on its type host *Pugettia producta.* Specimens of *Carcinonemertes* of uncertain affinities are also found on *Cancer antennarius, C. anthonyi* and *C. productus.*

3. *Carcinonemertes epialti* adults are egg predators on ovigerous hosts. Growth, demography and abundance are described in relation to the embryogenic stage of the host brood at Bodega Harbor, California.

4. Nonfeeding juveniles are ensheathed on individuals of both host sexes over 8.0 mm carapace width.

5. Transmission experiments show that contact transfer of juvenile nemerteans from males to other hosts may occur.

6. The percentage of infestation and mean density peak in autumn on *H. oregonensis* at Bodega Harbor.

7. Ovigerous female hosts are more frequently infested with *C. epialti,* particularly at small host sizes, than are male or nonovigerous female hosts at Bodega Harbor. However, average worm density on ovigerous females is low.

8. Mean density of *C. epialti* rises through late postmolt, declines during intermolt and rebuilds to a high level in late premolt *H. oregonensis* from Bodega Harbor.

9. Large crabs have a higher percentage of infestations and mean densities per infection than do small crabs. Nemerteans are more frequently found in the sternal-abdominal furrow and less frequently in the limb axillae on large crabs.

10. A model of *C. epialti* transmission and site occupancy is proposed, incorporating the influence of host size, sex, reproductive state, embryogenesis, molt cycle stage and molt cycle duration of *H. oregonensis* at Bodega Harbor. Site availability increases with host size. At higher densities the juvenile nemerteans increasingly occupy less preferred sites. Transferral of juvenile nemerteans occurs and is considered responsible for the high frequency of low infestation levels. Ovigerous females are more likely to be infested but with low density infestations.

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